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The La Voulte-sur-Rhône Lagerstätte (Middle Jurassic, France)

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ABSTRACT

The La Voulte Lagerstätte (Jurassic, France) is characterized by a diverse and exceptionally well-preserved fauna. It was located along the western Tethyan margin where the submarine relief was steep. The sedimentation was dominated by marls suggesting a low energy and deep-water depositional environment. The La Voulte biota is remarkable for its biodiversity with about 60 different species. The major components are the arthropods (50% of the species), the cephalopods (10%) and the echinoderms (10%). Among the arthropods, the composition and some anatomical features suggest a relatively deep-water environment characterized by dim-light conditions. The cephalopods and other organisms (pycnogonids, asterids), have extant analogues that all live in deep-water niches always exceeding 200 m. The fauna as a whole bears the characteristic features of the present-day bathyal fauna. The La Voulte Lagerstätte may be one of the rare Jurassic Lagerstätten, if not the unique, to have fossilized a deep marine fauna.

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R É S U M É

Le Lagerstätte de La Voulte (Jurassique, France) est un gisement à conservation exceptionnelle, appartenant à la marge passive de la Téthys occidentale, où la paléotopographie sous-marine était très escarpée. La sédimentation était essentiellement marneuse et suggère un milieu de dépôt calme sous une tranche d'eau importante. La faune de La Voulte présente une biodiversité remarquable, avec une soixantaine d'espèces recensées. Les organismes dominants sont les arthropodes (50% des espèces), les céphalopodes (10%) et les échinodermes (10%). Les arthropodes, par leur composition et leur anatomie fonctionnelle, suggèrent un milieu de vie profond où la luminosité était très faible, voire nulle. Les céphalopodes et d'autres organismes (pycnogonides, astérides) vivaient très vraisemblablement dans une tranche d'eau supérieure à 200 m, comme leurs représentants actuels. Le gisement de La Voulte est probablement un des rares Lagerstätten jurassiques, sinon le seul, à renfermer une faune de milieu marin profond.

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1. Introduction

Interest in the Middle Jurassic (Callovian) La Voulte Lagerstätte dates back to the middle 19th century and the pioneer works by Fournet (1843) who first mentioned the presence of articulated ophiuroids in this locality (Figs. 1 and 2). Indeed, this Konservat-Lagerstätte contains a diverse and remarkably preserved fauna dominated by ophiuroids and crustaceans, with also numerous soft-bodied organisms. By far, the most frequent animals of the La Voulte biota are the delicate brittle star *Ophiopinna elegans* (Fig. 2B) and small thin-shelled bivalves (*Bostrea buchii*), both found in large numbers on bedding planes. Crustaceans are represented by abundant decapods that are most frequently three-dimensionally preserved in sideritic nodules. More enigmatic and also very abundant at La Voulte, are the thylacocephalans that were unusually large bivalved arthropods armed with prehensile appendages and bearing huge visual organs. Both in terms of diversity and abundance, the arthropod fauna from La Voulte rivals that of the famous Solnhofen Lagerstätte. Soft-bodied organisms are represented by exceptional specimens of cirrate octopods and other coleoid cephalopods, vampire squids, marine worms and sea spiders.

Although several spectacular cases of soft-bodied preservation have been succinctly described over the years, no comprehensive analysis of the organisms and communities present in this exceptional biota has been made so far by using modern techniques and detailed comparisons with modern ecosystems. Equally surprising is the lack of knowledge concerning the palaeoenvironmental setting of the La Voulte Lagerstätte and the taphonomic processes involved in the exceptional preservation of the fauna. At the beginning of the 1980s, successive field campaigns conducted by the 'Muséum national d'histoire naturelle', Paris (Fischer, 2003), yielded a substantial amount of new fossil material and confirmed the exceptional richness of the La Voulte biota but, unfortunately, failed to provide precise information on the palaeoenvironmental parameters and ecological organization of the biota (Fig. 2C, D). Several factors have obviously hindered accurate palaeoenvironmental studies at La Voulte. These are the small size of exposures, an homogenous facies with very few sedimentological features, fossils concentrated within less than 5–6 m of marls and, above all, a tectonic configuration with steeply dipping (dip 60°).

Considering that previous studies were unsuccessful, Charbonnier et al. (2007b) focused on the adjacent and contemporaneous outcrop of the Ravin du Chénier (150 m from the La Voulte Lagerstätte) that offered better conditions of exposure (relatively thick deposits and larger outcrops). This locality yielded abundant and well-preserved siliceous sponges and small stalked crinoids that, via comparisons with their extant analogues, turned out to be important biological indicators of environmental conditions such as the water depth. In a second time, the La Voulte fauna was analyzed in terms of biodiversity, environment and ecology by Charbonnier et al. (2010).

Here, we propose a synthesis about the La Voulte Lagerstätte and its fauna in order to bring key-information on the

biodiversity of an assumed bathyal environment during the Middle Jurassic.

2. Geological setting and fossil localities

The La Voulte Lagerstätte and the nearby Ravin du Chénier are both located in south-eastern France (Ardèche) along the right bank of the Rhône River (150 km south of Lyon) and belong to the eastern sediment cover of the Massif Central (Fig. 1). The Massif Central is an Hercynian crystalline complex whose eastern margin was faulted and tilted during the Middle Jurassic. A major sub-vertical normal fault, the so-called La Voulte fault (N54°, inherited Hercynian direction) was very active during the Callovian and cuts through the whole area. The two studied localities (La Voulte Lagerstätte, Ravin du Chénier) are also separated by a transverse normal fault (the Col de Viau fault, N120°) with very limited horizontal displacement (25–50 m).

The most recent palaeogeographic reconstructions for the Callovian place the La Voulte area along the western margin of the Tethys Ocean and adjacent to the Massif Central which was probably submerged at that time (Enay et al., 1993). The Tethyan margin running east of La Voulte was characterized by a complex submarine palaeotopography of tilted blocks generated by a series of inherited Hercynian and transverse faults. Platforms lying on the submerged Massif Central were the principal source of carbonate sediments whereas terrigenous inputs originated partially from the submarine erosion of the Hercynian basement and its Early Mesozoic sediment cover (Elmi, 1990). The biostratigraphy of the La Voulte area (both Lagerstätte and Ravin du Chénier) was established by Elmi (1967) and is based on ammonite biozonation: the deposits of the two localities belong to the Early Callovian Gracilis Biozone.

The fossiliferous layers of the La Voulte Lagerstätte crop out in the Ravin des Mines south-western of the town of La Voulte-sur-Rhône and occur within a relatively thin interval (5–6 m). Their lithology consists of marls topped with 15 m thick iron deposits that were exploited in the 19th century (Ledoux, 1868). The basal marls contain numerous sideritic nodules which frequently preserve uncompact crustaceans and more or less undeformed soft-bodied cephalopods. Some marly horizons are also locally rich in soft-bodied fossils (e.g. cephalopods, worms) that occur more flattened. Thin iron carbonate layers with abundant ophiuroids occur throughout the succession. The deposits of the Ravin du Chénier crop out in badlands 150 m south-western of the La Voulte Lagerstätte and are separated from it by the Col de Viau transverse fault. They consist of 20 m of marls and marly limestones. The first 15 m of the section are characterized by alternations of marls and limestones yielding siliceous sponges and stalked crinoids. Abundant sponges occur in the uppermost 5 m of the section forming the "Lentille à hexactinellides" (Sayn and Roman, 1928). This conspicuous fossiliferous horizon is overlain by very limited black layers rich in black phosphatized ammonites, followed by thin iron carbonate layers and slumped calcareous beds possibly generated by synsedimentary slides.

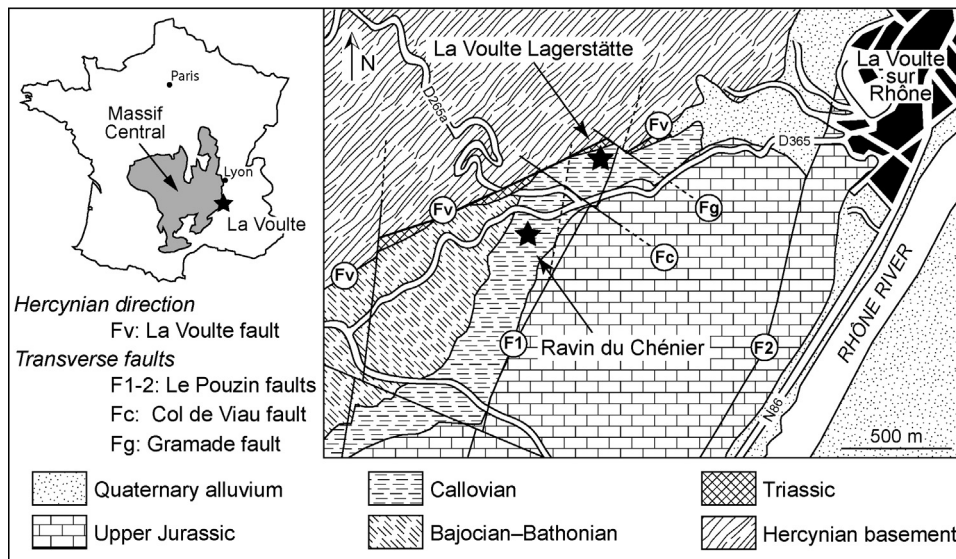


Fig. 1. La Voulte Lagerstätte (Middle Jurassic, France): location and geological setting (modified from Charbonnier et al., 2010).

Fig. 1. Lagerstätte de La Voulte (Jurassique moyen, France): localisation et contexte géologique (modifié d'après Charbonnier et al., 2010).

3. Ravin du Chénier

3.1. Siliceous sponges

Charbonnier et al. (2007b) studied the siliceous sponges and the stalked crinoids from the Ravin du Chénier and provided evidence of a deep-water setting for the La Voulte Lagerstätte (Fig. 3). The siliceous sponges from the Ravin du Chénier were first described by Dumortier (1871) and revised by Moret (1928) who established systematic inventories. These sponges are not preserved in life position and are found scattered in sediments. However, many delicate specimens such as branching and narrow tubular like ones are complete and a number of them have their basal attachment preserved. Rare basal attachments on fragments of crystalline rocks provide evidence that these sponges grew on the submarine exposed areas of the crystalline basement. Their original habitat was obviously situated at some distance from their depositional area which is overwhelmingly dominated by marls. Their excellent preservation, however, is not consistent with a post-mortem transportation driven by high-energy currents. The siliceous sponge fauna of the Ravin du Chénier was interpreted to be parautochthonous. This fauna consists of hexactinellids (ca 80% of the fauna) and lithistids (ca 20%).

According to Charbonnier et al. (2007b) and Charbonnier (2009), a series of fossil evidence supported by detailed comparisons with modern and fossil morphological and ecological analogues underpins the notion that the sponge communities of the Ravin du Chénier once flourished in dysphotic or aphotic, relatively deep, possibly bathyal settings. These are: (1) the dominance of hexactinellids that, in extant marine environments, characterizes deeper water conditions, (2) the presence of lithistids and especially rhizomorines whose modern representatives occur mostly in the bathyal zone; (3) the prevalence of conical shapes erect morphologies

that typifies most of modern deep-sea sponges; (4) the absence of low and flat morphotypes that usually thrived in Late Jurassic circalittoral environments; (5) the lack of photophilic organisms encrusting the upper part of the external wall of sponges and the lack of sciophilous (=capable of thriving in shade) epizoans in parts facing downwards. This feature does not indicate a precise bathymetrical range but is consistent with dysphotic or aphotic conditions. The benthic environment of the Ravin du Chénier was obviously much deeper than the circalittoral zone and may correspond to the slope-basin transition probably in the upper bathyal zone (200–400 m). The mode of attachment of certain sponges (those with an encrusting base on crystalline rock) provides some clues concerning the bottom conditions that once prevailed in the Ravin du Chénier. It suggests the existence of both submarine exposures of crystalline rocks and muddy areas where the sponges were preserved. The crystalline exposures may find their origin in the major fault of La Voulte and the fault complex associated with it. The fault system is likely to have played a key-role in creating a submarine palaeotopography with substantial breaks and steep reliefs that favoured the colonization by siliceous sponges. Such substrate and topographic heterogeneity is typical of the extant bathyal slope environments that are characterized by a relatively steep relief, and are scoured by currents and mudflows.

3.2. Stalked crinoids

The stalked crinoids were first reported to occur in the Ravin du Chénier by Sayn and Roman (1928). According to Charbonnier et al. (2007b), the fauna consists of cyrtocrinids with a lesser proportion of isocrinids. Cyrtocrinids are small, stalked and sturdy crinoids (length 4–5 cm) with short arms that can be enrolled for protection. The aboral cup may be asymmetric. The stem is short with few



Fig. 2. (Colour online). Historical work on the La Voulte Lagerstätte. A, Joseph Fournet (1801–1869), Professor of Geology at the University of Lyons, wrote one of the first descriptions of the outcrop. B, *Ophiopinna elegans* (complete specimen, UJF-ID.11923), small brittle star very abundant in the La Voulte sediments. C–D, Palaeontological excavations (1983–1986) organized by Professor Jean-Claude Fischer from the 'Muséum national d'histoire naturelle', Paris. Scale bar: 1 cm. Collections: UJF-ID: Université de Grenoble.

Fig. 2. (Couleur en ligne). Travaux historiques sur le Lagerstätte de La Voulte. A, Joseph Fournet (1801–1869), Professeur de géologie à la faculté des sciences de Lyon, écrit une des premières descriptions du site. B, *Ophiopinna elegans* (spécimen complet, UJF-ID.11923), petite ophiure très abondante dans les sédiments de La Voulte. C–D, fouilles paléontologiques (1983–1986), organisées par le professeur Jean-Claude Fischer, du Muséum national d'histoire naturelle, Paris. Échelle : 1 cm. Collection : UJF-ID = Université de Grenoble.

columnals and its distal end cemented to the substrate. By contrast, isocrinids display a long heteromorphic stem surmounted by a rather small and low cup with a long multiarmed crown. Brachial crown works in currents like a parachute. Their length generally exceeds 10 cm.

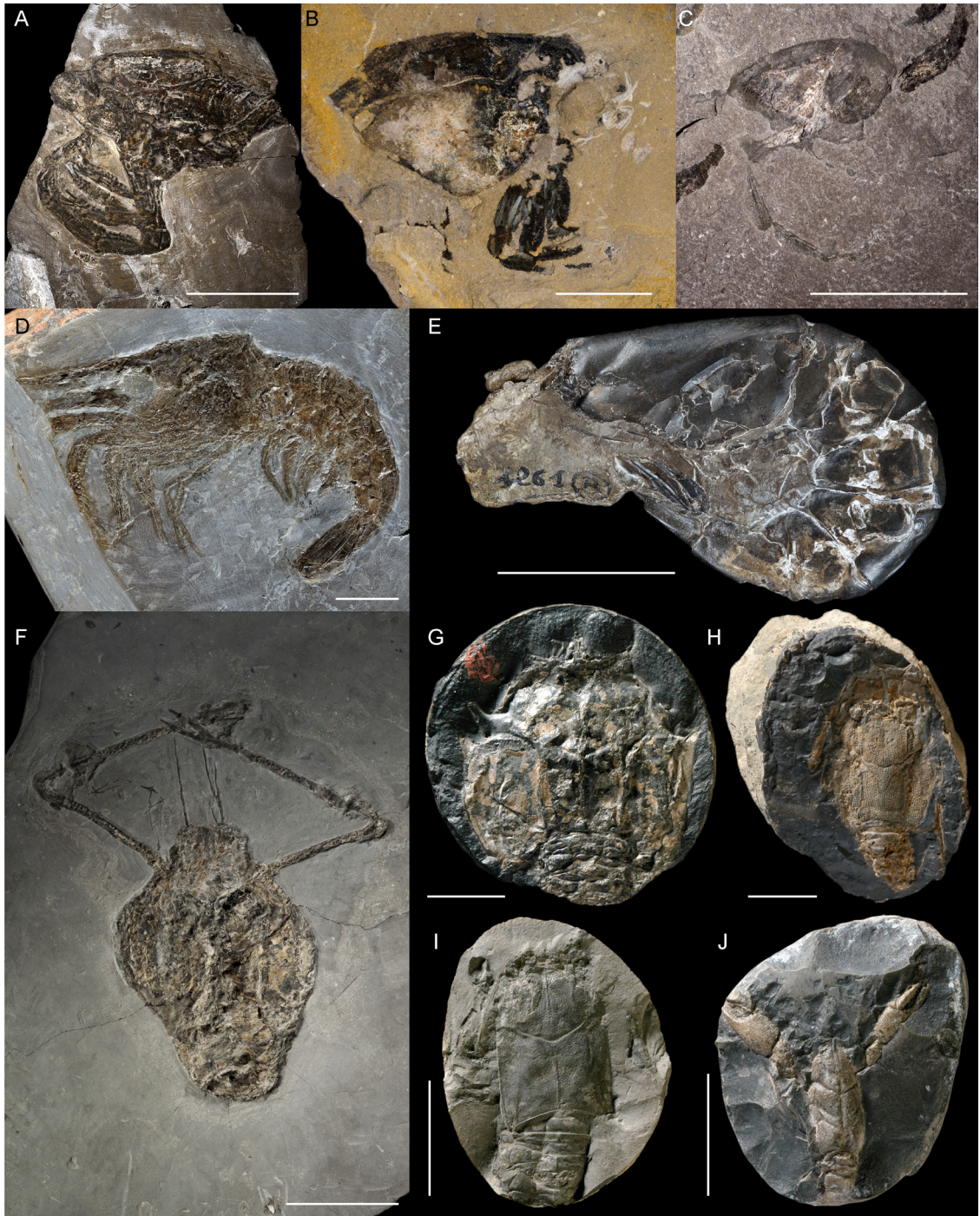
The cyrtocrinids from the Ravin du Chénier are represented by isolated remains (cups, brachials, columnals and holdfasts; Fig. 3I–N) that fall within three different families: (1) the Eugeniocrinitidae with *Eugeniocrinus dumortieri* and *Lonchocrinus* sp., (2) the Sclerocrinitidae with *Cyrtocrinus nutans*, *C. nutans* var. *voultensis* and

Gammarocrinites compressus and, (3) the Phyllocrinidae with *Phyllocrinus colloti*. Additionally, *Dolichocrinus aberrans* is a rare small crinoid of uncertain affinities although superficially resembling cyrtocrinids. *Cyrtocrinus nutans* (71% of cyrtocrinid remains) is numerically the most abundant species. The cyrtocrinid elements present a low degree of attrition. Columnal surfaces, brachial facets and cup surfaces are neither abraded nor rounded or bio-eroded. Similar with their sponge associates, cyrtocrinids are most likely autochthonous or parautochthonous, their habitat lying probably close to their area of deposition. Based upon



Fig. 3. (Colour online). Siliceous sponges (A–H) and cyrtocrinid crinoids (I–N) from the Ravin du Chénier. A, *Craticularia parallela* (FSL 710010). B, *Gevreya synthetica* (UJF-ID), note the encrusting base. C, *Stauroderma inversa* (FSL 710008). D, *Craticularia parallela* (FSL 710013). E, *Moretispongia praegnans* (UJF-ID). F, *Verruculina multiforis* (FSL 710004). G, *Craticularia parallela* (FSL 710011). H, *Craticularia parallela* (FSL 710012). I, *Eugeniocrinus dumortieri* (FSL 710036), cup. J, *Cyrtocrinus nutans* (FSL 710040), spoon-like cup with fused proximal columnals. K, *Cyrtocrinus nutans* var. *voultensis* (FSL 710044), asymmetric cup. L, *Gammarocrinites compressus* (FSL 710045), cup. M, *Dolichocrinus aberrans* (FSL 710049) cup with fused proximal stem. N, *Phyllocrinus colloti* (FSL 710051) cup. Vertical scale bars: 2 cm; horizontal scale bars: 2 mm. Collections: FSL = Université Lyon-1; UJF-ID = Université de Grenoble.

Fig. 3. (Couleur en ligne). Éponges siliceuses (A–H) et crinoïdes cyrtocrinidés (I–N) du ravin du Chénier. A, *Craticularia parallela* (FSL 710010). B, *Gevreya synthetica* (UJF-ID), noter la base encroûtante. C, *Stauroderma inversa* (FSL 710008). D, *Craticularia parallela* (FSL 710013). E, *Moretispongia praegnans* (UJF-ID). F, *Verruculina multiforis* (FSL 710004). G, *Craticularia parallela* (FSL 710011). H, *Craticularia parallela* (FSL 710012). I, *Eugeniocrinus dumortieri* (FSL 710036), calice. J, *Cyrtocrinus nutans* (FSL 710040), calice en forme de cuillère, avec des columnales proximales fusionnées. K, *Cyrtocrinus nutans* var. *voultensis* (FSL 710044), calice asymétrique. L, *Gammarocrinites compressus* (FSL 710045), calice. M, *Dolichocrinus aberrans* (FSL 710049) calice avec pédoncule proximal fusionné. N, *Phyllocrinus colloti* (FSL 710051) calice. Échelles verticales : 2 cm ; échelles horizontales : 2 mm. Collections : FSL = Université Lyon 1 ; UJF-ID = Université de Grenoble.



morphological and ecological comparisons with extant crinoids, Charbonnier et al. (2007b) provided compelling evidence that the crinoids from the Ravin du Chénier lived in relatively deep-sea habitats (at least exceeding 200 m). These are: (1) the dominance of cyrtocrinids almost identical to the extant bathyal representatives of the group and (2) the presence of *Dolichocrinus* and *Balanocrinus* that closely resemble typical extant deep-sea crinoids (the Bathycrinidae and the Isocrinidae Balanocrininae, respectively). *Cyrtocrinus nutans* that dominates the crinoid assemblages of the Ravin du Chénier, may have occupied, along with others robust cyrtocrinids, habitats and ecological niches comparable with those of the extant *Gymnocrinus richeri* (relatively small endemic populations colonizing bathyal seamounts and hardgrounds where energy is high).

4. La Voulte Lagerstätte

4.1. Palaeobiodiversity

An updated faunal inventory of the La Voulte Lagerstätte has been proposed in the monograph of Charbonnier (2009) (Figs. 4 and 5, Table 1). The fauna consists of about 60 different species among which the most typical elements are the arthropods (30 species), the cephalopods (7 species, except ammonites), the marine worms (7 species), the echinoderms (ophiuroids and sea stars, 6 species), the vertebrates (marine crocodile, and sharks, 4 species), the bivalves (2 species) and the brachiopods (2 species).

4.1.1. Arthropods

The arthropods are the most abundant and diversified organisms (Charbonnier et al., 2010; Van Straelen, 1922, 1923a, 1923b, 1925). They occur either in early diagenetic concretions where they are three-dimensionally preserved or in surrounding marls where they are preserved as pyritized and phosphatized bodies more or less flattened. The La Voulte arthropod fauna as a whole includes 30 different species assigned to the thylacocephalans (Fig. 4A–C), the crustaceans (Fig. 4D–J) and the pycnogonids (Fig. 5A). The crustaceans are the most diversified group with 23 species distributed in a dozen families (e.g., Penaeidae, Eryonidae, Mysidae). The thylacocephalan

arthropods are represented by 4 species (Secrétan, 1983, 1985; Secrétan and Riou, 1983): *Dollocaris ingens* (Fig. 4A), *Kilianicaris lerichei* (Fig. 4B), *Clausocaris ribeti* (Fig. 4C) and *Paraostenia vouldensis*. Decapods (17 species) are remarkably diverse and most species such as *Aeger brevisrostris* (Fig. 4D), *Archeosolenocera straeleni* (Fig. 4E), '*Coleia*' *gigantea* (Fig. 4F), *Eryon ellipticus* (Fig. 4G), *Willemoesiocaris ovalis* (Fig. 4H), *Hellerocaris falloti* (Fig. 4I), *Eryma mandelslohi* (Fig. 4J) and *Eryma cumonti* are typical of the La Voulte Lagerstätte. Mysidaceans (Lophogastrida: 2 species; Mysida: 2 species) and cumaceans (1 species) are less diversified (Bachmayer, 1960; Secrétan and Riou, 1986). Recently Charbonnier et al. (2013) described also a new glypheid lobster preserved in a concretion: *Glypheopsis vouldensis*.

The pycnogonids (sea spiders) are very rare in the fossil record. The La Voulte sea spiders (Arthropoda: Pycnogonida) fill a 400-million-year gap of knowledge in the evolutionary history of these enigmatic marine arthropods that constitute today a small group of more than 1300 described species. The three species (*Colossopantopodus boissinensis*, *Palaeopycnogonides gracilis*, *Palaeoendeis elmii*) of pycnogonids from the La Voulte Lagerstätte provide altogether the most detailed information so far available on the morphology, mode of life and habitats of Mesozoic sea spiders. They reveal very close morphological and functional (locomotion, feeding) similarities with present-day pycnogonids (e.g. Ammotheidae, Colossendeidae, Endeidae) and, by contrast, marked differences with the Palaeozoic representatives of the group. The results of Charbonnier et al. (2007a) point to a remarkable morphological and ecological stability of this arthropod group over at least 160 million years and suggest that the colonization of the deep-sea by pycnogonids occurred before the Jurassic.

4.1.2. Echinoderms

Villier et al. (2009) described the asteroid fauna in details. A small, stellate specimen is assigned to *Terminaster cancriformis*, a species already known from Jurassic clay deposits of Germany, Switzerland and England. The morphology of *Terminaster* illustrates mostly plesiomorphic features for post-Paleozoic sea stars, and the genus may be considered either as a paedomorphic Zoroasteridae or a stem group Forcipulatacea. The small asteroid

Fig. 4. (Colour online). Thylacocephalans (A–C) and decapod crustaceans (D–J) from the La Voulte Lagerstätte. A, *Dollocaris ingens* (MNHN.F.R06203), complete specimen with raptorial appendages and protruding eyes, left lateral view. B, *Kilianicaris lerichei* (MNHN.F.R50972), subcomplete specimen, right lateral view. C, *Clausocaris ribeti* (MNHN.F.A29149), complete specimen, right lateral view. D, *Aeger brevisrostris* (MNHN.F.R61853) subcomplete specimen. E, *Archeosolenocera straeleni* (MNHN.F.R61863) subcomplete specimen preserved in volume. F, '*Coleia*' *gigantea* (MSNM i20703) complete specimen with long and slender first pair of pereopods, ventral view. G, *Eryon ellipticus* (UJF-ID.11540, holotype), carapace and pleonites 1–3, dorsal view. H, *Willemoesiocaris ovalis* (UJF-ID.11542, holotype), dorsal view. I, *Hellerocaris falloti* (UJF-ID.11553) carapace and pleonites 1–4, dorsal view. J, *Eryma mandelslohi* (UJF-ID.11543), subcomplete specimen dorsal view. Scale bars: 1 cm (B), 2 cm (C–E, G–J), 5 cm (A, F). Collections: MNHN.F = Muséum national d'histoire naturelle, Paris; UJF-ID = Université de Grenoble; MSNM = Museo di Storia Naturale di Milano.

Fig. 4. (Couleur en ligne). Thylacocéphales (A–C) et crustacés décapodes (D–J) du Lagerstätte de La Voulte. A, *Dollocaris ingens* (MNHN.F.R06203), spécimen complet, avec appendices raptoriaux et yeux protubérants, vue latérale gauche. B, *Kilianicaris lerichei* (MNHN.F.R50972), spécimen subcomplet, vue latérale droite. C, *Clausocaris ribeti* (MNHN.F.A29149), spécimen complet, vue latérale droite. D, *Aeger brevisrostris* (MNHN.F.R61853) spécimen subcomplet. E, *Archeosolenocera straeleni* (MNHN.F.R61863) spécimen subcomplet préservé en volume. F, « *Coleia* » *gigantea* (MSNM i20703) spécimen complet avec une première paire de péréiopodes longs et fins, vue ventrale. G, *Eryon ellipticus* (UJF-ID.11540, holotype), carapace et pléonites 1–3, vue dorsale. H, *Willemoesiocaris ovalis* (UJF-ID.11542, holotype), vue dorsale. I, *Hellerocaris falloti* (UJF-ID.11553) carapace et pléonites 1–4, vue dorsale. J, *Eryma mandelslohi* (UJF-ID.11543), spécimen subcomplet, vue dorsale. Échelles : 1 cm (B), 2 cm (C–E, G–J), 5 cm (A, F). Collections : MNHN.F = Muséum national d'histoire naturelle, Paris ; UJF-ID = Université de Grenoble ; MSNM = Museo di Storia Naturale di Milano.

Table 1

List of the taxa preserved in the La Voulte Lagerstätte (Middle Jurassic, France).

Tableau 1

Liste des taxons préservés dans le Lagerstätte de La Voulte (Jurassique moyen, France).

ARTHROPODA**Crustacea**

- Antrimpos secretaniae* Carriol & Riou, 1991
Aeger brevisrostris Van Straelen, 1923
Archeosolenocera straeleni Carriol & Riou, 1991
 "Coleia" gigantea Van Straelen, 1923
Eryma cumonti Van Straelen, 1921
Eryma mandelslohi Meyer, 1837
Eryon ellipticus Van Straelen, 1923
Eucopia praecursor Secrétan & Riou, 1986
Glypheopsis vouldensis Charbonnier, Garassino, Schweigert & Simpson, 2013
Hellerocaris falloti Van Straelen, 1925
Lophogaster vouldensis Secrétan & Riou, 1986
Palaeocuma hessi Bachmayer, 1960
Rhodanicaris depereti Van Straelen, 1925
Siriella antiqua Secrétan & Riou, 1986
Siriella carinata Secrétan & Riou, 1986
Stenochirus vahldieki Schweigert, Garassino & Riou, 2006
Udora gevreyi Van Straelen, 1923
Udora minuta Van Straelen, 1923
Willemoesiocaris ovalis Van Straelen, 1923

Thylacocephala

- Clausocaris ribeti* (Secrétan, 1985)
Dollocaris ingens Van Straelen, 1923
Kilianicaris lerichei Van Straelen, 1923
Paraostenia vouldensis Secrétan, 1985

Pycnogonida

- Colosspantopodus boissinensis* Charbonnier, Vannier & Riou, 2007
Palaeoendeis elmii Charbonnier, Vannier & Riou, 2007
Palaeopycnogonides gracilis Charbonnier, Vannier & Riou, 2007

MOLLUSCA**Cephalopoda**

- Gramadella piveteaui* Fischer & Riou, 1982
Hibolites hastatus Montfort, 1808
Proteroctopus ribeti Fischer & Riou, 1982
Rhomboteuthis lehmani Fischer & Riou, 1982
Romaniteuthis gevreyi (Roman, 1928)
Teudopsis sp.
Vampyronassa rhodanica Fischer & Riou, 2002

Bivalvia

- Bositra buchi* (Roemer, 1836)
Plagiostoma sp.

BRACHIOPODA

- Rhynchonelloidella spathica* (Lamarck, 1819)
Robustirhynchia tenuiformis Seifert, 1963

ECHINODERMATA**Ophiuroidea**

- Ophiopinna elegans* (Heller, 1858)

Asteroidea

- Terminaster cancriformis* (Quenstedt, 1876)
Decacuminaster solaris Villier, Charbonnier & Riou 2009

Crinoidea

- Pentacrinus* sp.
Rhodanometra lorioli Manni, Nicosia & Riou, 1985

Echinoidea

- Rhabdocidaridaris spinosa* (Agassiz, 1840)

ANNELIDA

- Iubarenicola fisheri* Alessandrello, Bracchi & Riou, 2004
Paleoaphrodite adeliae Alessandrello, Bracchi & Riou, 2004
Paleoaphrodite briggsiana Alessandrello, Bracchi & Riou, 2004
Paleoaphrodite gallica Alessandrello, Bracchi & Riou, 2004
Protophloe rhodanitis Alessandrello, Bracchi & Riou, 2004
Rondeletia scutata Alessandrello, Bracchi & Riou, 2004

HEMICHORDATA

- Megaderaion callovianum* Alessandrello, Bracchi & Riou, 2004

VERTEBRATA**Actinopterygii**

- Pholidophorus* sp.
Macrosemius sp.
Ophiopsis sp.

Sarcopterygii

- Holophagus* sp.

Crocodylia

- Metriorhynchus* sp.

Terminaster cancriformis is considered to be a very primitive taxon to the Forcipulatida and maybe to the entire crown group. The overall shape is similar to that of the extant bathyal Zoroasteridae and Neomorphasteridae, which suggests a generalist but primarily carnivorous nutrition in *T. cancriformis*. Two specimens of a large multiarmed sea star are assigned to *Decacuminaster solaris* (Fig. 5B), characterized by a lack of abactinal plates and an axial skeleton typical of the Velatida, including the fossil clade Palaeobenthoplectininae. The sea stars of La Voulte are morphologically relatively similar to modern bathyal forms, although they are taxonomically distinct. In modern Oceans, the association of a multiarmed Velatida and a zoroasterid-like species would be typical of bathyal/abyssal environments, which suggests that these groups explored deep sea environments early in their history.

4.1.3. Cephalopods

The coleoid cephalopod fauna includes seven species assigned to the octopods, the vampire squids and the teuthoids. Octopods are represented by the very famous

and unique *Proteroctopus ribeti* (Fig. 5C; see Fischer and Riou, 1982a for details). Vampire squids are represented by about 20 specimens attribute to *Vampyronassa rhodanica* (Fig. 5D; Fischer and Riou, 2002), the oldest representative of the Vampyromorpha. Four species of teuthoid squids are only described at La Voulte (Fischer and Riou, 1982b): *Romaniteuthis gevreyi*, *Rhomboteuthis lehmani* (Fig. 5E), *Teudopsis* sp., *Gramadella piveteaui*.

4.2. Palaeoecology

The arthropods—the most abundant and diversified organisms—are used by Charbonnier et al. (2010) as an important source of information to reconstruct key aspects of the La Voulte marine palaeoenvironment. Quantitative analyses based on the specimens preserved in nodules pointed out four dominant groups: (1) the thylacocephalans (32.5% of nodules), (2) the Solenoceridae shrimps (22.4%), (3) the polychelidan lobsters (15.5%) and (4) the Penaeidae shrimps (9.3%). The thylacocephalans are enigmatic “bivalved” arthropods with a distinctive morphology



Fig. 5. (Colour online). Exceptionally preserved specimens from the La Voulte Lagerstätte. A, *Palaeopycnogonides gracilis* (holotype), dorsal view. B, *Decacaminaster solaris* (paratype), asteroid bearing 18 arms. C, *Proteroctopus ribeti* (holotype MNHN.F.R03801), octopod with pyritisation of the soft parts. D, *Vampyronassa rhodanica* (paratype MNHN.F.B74243) vampire squid. E, 3D-preserved teuthoid cephalopod within marly sediment (*Rhomboteuthis lehmani*, paratype MNHN.F.R03761). F, *Paleoaophrodite gallica* (holotype, MNHN.F.B48342), phospatized compression. Scale bars: 2 cm. Collections: MNHN.F = Muséum national d'histoire naturelle, Paris.

Fig. 5. (Couleur en ligne). Spécimens du Lagerstätte de La Voulte montrant une préservation exceptionnelle. A, *Palaeopycnogonides gracilis* (holotype), vue dorsale. B, *Decacaminaster solaris* (paratype), noter les 18 bras. C, *Proteroctopus ribeti* (holotype MNHN.F.R03801), octopode avec pyritisation des parties molles. D, *Vampyronassa rhodanica* (paratype MNHN.F.B74243), vampyromorphe. E, Céphalopode teuthoïde préservé en volume (*Rhomboteuthis lehmani*, paratype MNHN.F.R03761). F, *Paleoaophrodite gallica* (holotype MNHN.F.B48342), empreinte phospatée. Échelles : 2 cm. Collections : MNHN.F = Muséum national d'histoire naturelle, Paris.

characterized at La Voulte by hypertrophied visual organs and long raptorial appendages. In the nodules, the most frequent and well-preserved species is *Dollocaris ingens* (Fig. 4A). This species presents a wide range of sizes from probable juvenile specimens to adult ones. The association

in situ of these different stages of growth probably indicates autochthonous assemblages. The main palaeoecological interpretations are based on *D. ingens* which is presently the best known species. The prominent eyes of *D. ingens* were preliminarily studied by Fröhlich et al. (1992) who

show the three-dimension preservation of the visual organs and some of their features such as the presence of numerous small ommatidia distributed over huge eyes. The high density of ommatidia suggests well-developed visual capacities. Thus the vision of *D. ingens* seems straightly linked to a predatory behaviour. In addition, the eyes of *D. ingens* resemble superficially the hypertrophied eyes of some extant deep-living hyperiid amphipods. Relatively voluminous eyes are also typical of numerous deep-sea crustaceans (Hiller-Adams and Case, 1985). Thus, the giant eyes of *D. ingens* suggest dim-light conditions and probably a relatively deep-water environment most probably exceeding 200 m (= bathyal zone). *D. ingens* is considered as a predator (Vannier et al., 2006) and this hypothesis is confirmed by several singular anatomic features such as (1) the hypertrophied eyes that suggest a relatively deep and dark environment where the detection of prey and other possible predators is essential; (2) the very robust raptorial appendages which the largest pair is often spiny and that might probably quickly spread forwards to catch and tear up preys.

The dendrobranchiate shrimps (Decapoda) are the second dominant group of arthropods. Two families are represented: the Solenoceridae (22.4% of specimens) and the Penaeidae (9.3%). By far, *Aeger breviostris* (Fig. 4D) and *Archeosolenocera straeleni* (Fig. 4E) are the most frequent species. *Archeosolenocera straeleni* is considered as the only fossil representative of the extant family Solenoceridae (Carriol and Riou, 1991).

This species is relatively similar in proportions and general morphology to several extant Solenoceridae and Aristeidae shrimps and may be a benthic shrimp living on a muddy substrate that is compatible with the marly sediments of the La Voulte Lagerstätte. *Aeger breviostris* is a relatively similar in size and general morphology to some extant Aristeidae shrimps such as *Aristeomorpha foliacea* or *Aristaopsis edwardsiana*. These giant red shrimps are deep-water organisms actively fished along the continental slope at depths ranging from 300 to 700 m where their peaks of abundance are reached (Guégen, 1998). They live on muddy grounds and move in dense aggregates along the steep reliefs and the submarine canyons of the continental slope (Bianchini and Ragonese, 1994; Pérez Farfante, 1988). *Aeger breviostris* might be a benthic shrimp moving on muddy substrate typical of the marly sediments of La Voulte in which it is often preserved in association with *Archeosolenocera straeleni*. More precisely, according to Charbonnier et al. (2010), *Aeger breviostris* was most probably nectobenthic as its long pleopods suggest well-developed capacities for swimming.

The polychelidan lobsters (15.5% of the specimens) are the third dominant group of the La Voulte arthropods. They include four species: (1) *Coleia gigantea* (Fig. 4F), one of the largest known coleiiids, its abundance at La Voulte suggests it was probably gregarious and autochthonous; (2) *Eryon ellipticus* (Fig. 4G), the oldest species of *Eryon*—a genus well-known in the Late Jurassic of southern Germany (Charbonnier et al., 2012); (3) *Willemoesiocaris* (Fig. 4H), the oldest occurrence of the Polychelidae—the family containing all extant species of polychelidan lobsters and only one other fossil species (Aguirre-Urreta et al., 1990); and

(4) *Hellerocaris falloti* (Fig. 4I), currently ascribed to the Coleiidae—its peculiar morphology suggests it probably belongs to a phylogenetic lineage distinct from currently recognized polychelidan families.

Study of polychelidan lobsters from La Voulte is far from finished. In addition to necessary revision of the described species, at least four additional morphotypes have been discovered. They include: (1) small coleiiids that may represent juveniles of *Coleia gigantea*; (2) an undescribed species of coleiid with exceptionally large eyes, confirming the palaeoenvironmental interpretation of La Voulte as a deep-water ecosystem; (3) an undescribed species of eryonid with a peculiar trapezoidal cephalothorax; (4) and last but not least, the oldest occurrence of *Cycleryon*, a genus previously only reported from the Late Jurassic of southern Germany and South-East France (Audo et al., 2014; Charbonnier and Garassino, 2012; Garassino and Schweigert, 2006). In conclusion, the study of the La Voulte polychelidan lobsters reveals two important characteristics of this fauna: its phylogenetic and morphological diversity and an unsuspected link with the Late Jurassic German and French faunas that were preserved from shallower palaeoenvironments. For these reasons, there is undoubtedly much to learn about the evolutionary history and palaeoecology of polychelidan lobsters in La Voulte.

4.3. Palaeoenvironment

4.3.1. Comparisons with other Jurassic Lagerstätten

The high proportion of arthropods (50% of the species richness) makes the La Voulte fauna a very original assemblage that rivals that of the celebrate Solnhofen Lagerstätte (Barthel, 1978; Frickhinger, 1994, 1999; Garassino and Schweigert, 2006). Because of their specific richness (30 species), their abundances (hundreds of specimens) and their originality (10–12 species only described at La Voulte), the La Voulte arthropods may be considered as the richest and the most complete fauna after that of Solnhofen. The La Voulte fauna, however, presents relatively low diversity in front of the high species richness generally observed in other Mesozoic Lagerstätten such as Holzmaden (Toarcian; Gall and Blot, 1980; Hauff, 1960), Solnhofen (Kimmeridgian–Tithonian) or Cerin (Kimmeridgian). These differences of biodiversity must be balanced by the sampling methods and the outcrop surfaces. The fossiliferous beds from La Voulte crop out only in the Ravin des Mines (some hectares) and occur within a relatively thin interval whereas for instance, the Solnhofen limestones, intensely quarried for centuries, comprise a large set of localities extending over several hundreds of square kilometres (Barthel, 1978). The low biodiversity of the fauna from La Voulte is possibly linked to reduced outcrops but more certainly reflects major differences in palaeoecological and palaeoenvironmental conditions. Indeed, the lithographic limestones were deposited in very shallow carbonate platforms and coastal lagoons where high biodiversity is classically observed such as in southern Germany (Eichstätt, Solnhofen), in Lebanon (Hakel, Hadjula, Sahel Alma; see Gayet et al., 2003 for instance) or in France (Cerin, Canjuers; Bernier et al., 1991). By contrast, the four

dominant arthropod groups (thylacocephalans, Solenoceridae and Penaeidae shrimps, Coleiidae) presently studied suggest that during Callovian, the La Voulte area most likely laid under a water depth exceeding 200 m (= bathyal zone) with dysphotic or aphotic conditions.

4.3.2. Possible hydrothermal origin of the La Voulte fauna

The La Voulte fauna is remarkable by its composition and its high concentration of fossils occurring in very thick and localized deposits. This *in situ* fauna with abundant specimens and mainly dominated by arthropods is relatively uncommon in the recent environments. Thus, the La Voulte community may evoke some recent submarine hydrothermal assemblages such as those of the hydrothermal vents or of the cold seeps (Desbruyères et al., 2000, 2001). These deep-sea hydrothermal settings are characterized by high biomass and relatively low diversity. They are inhabited by dense macrofaunal communities commonly rich in large-sized bivalves, marine worms and diverse crustaceans. These faunas are considered as oases that contrast with the surrounding environments characterized by low population densities, low biomass and high species diversity (Sibuet and Olu, 1998). They are dependent of the hydrothermal activity that provides the energy necessary to the settlement and the preservation of these complex ecosystems. By comparison with these recent hydrothermal communities, the La Voulte Lagerstätte might correspond to a fossil oasis possibly linked to hydrothermal activity. This hypothesis is supported by different arguments such as (1) the high abundance of arthropods very similar to some remarkable concentrations of crustaceans specific to extant hydrothermal vents (Rona et al., 1986; Segonzac, 1992; Segonzac et al., 1993) and (2) the probable high endemism of the La Voulte arthropod fauna that comprise 10–12 species only described in this Lagerstätte. These species may represent highly adapted species as commonly observed in numerous deep-sea hydrothermal settings where 82% of species appear to be endemic (McArthur and Tunnicliffe, 1998; Van Dover, 2000). Although direct evidence of hydrothermal vents at La Voulte has not been found yet, the hydrothermal hypothesis is also supported by mineralogical and sedimentological clues. The presence of substantial iron deposits (thickness: 15 m) clearly related to the activity of the La Voulte fault reinforces the hypothesis of hydrothermal activity (Fournet, 1843; Wilby et al., 1996). Moreover, many of the minerals (e.g., pyrite, siderite, galena, sphalerite) preserving the La Voulte arthropods are often present at marine hydrothermal settings where fluids issuing onto the sea floor are enriched in various metals (especially Fe, Zn, Cu, and Mn; Little and Vrijenhoek, 2003; Little et al., 2004). In summary, a possible occurrence of hydrothermal activity in the vicinity of the La Voulte Lagerstätte may create conditions favourable to the settlement of specific marine community dominated by arthropods. This activity might be also at the origin of the exceptional preservation of the arthropods by the introduction in the environment of high concentrations of dissolved metals, sulphides and sulphates inducing early diagenetic mineralization.

5. Bathyal palaeoecosystem

Charbonnier et al. (2006, 2007b) and Charbonnier (2009) provided the first reconstructions of the La Voulte area during Jurassic that showed the assumed relations between the La Voulte Lagerstätte and the Ravin du Chénier. The palaeoenvironmental setting is tentatively placed within the bathyal zone which is consistent with the faunal composition of the La Voulte Lagerstätte and that of the Ravin du Chénier. Indeed, the La Voulte fauna contains vampire squids, cirrate octopods, sea spiders, great span sea stars and varied crustaceans that are all indicators of relatively deep-sea conditions. The enigmatic thylacocephalans bearing hypertrophied visual organs resembling those of deep-sea crustaceans, if not direct indicators of palaeobathymetry, clearly point to the dysphotic or aphotic conditions. Convergent palaeoenvironmental evidence obtained from both stalked crinoids, siliceous sponges from the Ravin du Chénier supports the hypothesis that the La Voulte area was situated in the bathyal zone, around the slope-basin transition.

The overall submarine topography is seen as being dominated by steep blocks generated and controlled by the La Voulte fault and its cortège of transverse faults. The La Voulte fault appears as a major break in the submarine topography of the Callovian palaeo-slope. Siliceous sponges and cyrtocrinids most probably inhabited this type of environment because it provided them appropriate hydrodynamic conditions and adequate substrates. In addition, this fault-controlled escarpment may have generated local sedimentary slides leading to parautochthonous burial of sponges and crinoids. This setting was certainly favourable to numerous other organisms present in the Ravin du Chénier such as sea stars, brachiopods, bivalves, ammonites or, belemnites. The block to which the present-day La Voulte Lagerstätte belongs, possibly benefited from local specific conditions that allowed the exceptional preservation of a vast array of organisms (e.g. deep-sea cephalopods, varied crustaceans, ophiuroids, sea stars and sharks). These favourable conditions may have been induced by the vicinity of hydrothermal vents. Although direct evidence for such vents has not been found yet, the presence of substantial iron deposits clearly related to the activity of the La Voulte fault brings some support to the hypothesis of hydrothermal activity. The fossil assemblages from the La Voulte Lagerstätte and the Ravin du Chénier are virtually contemporaneous and have a similar bathymetry. Their major differences may be explained by the occurrence of hydrothermal activity in the vicinity of the Lagerstätte area that created conditions favourable to: (1) the settlement of a specific community of organisms and, (2) the exceptional preservation of the fauna. These conditions were most probably absent in the Ravin du Chénier and allowed neither the colonization of the area by the same organisms as those from the Lagerstätte, nor soft-bodied preservation. Another possible effect of the hydrothermal activity on the marine fauna is the high concentration of flocculent metal minerals that possibly inhibited the development of sponges and crinoids in the La Voulte Lagerstätte area.

6. The future of the Lagerstätte

Considering its remarkable richness and international standing the La Voulte Lagerstätte is a unique site requiring conservation measures and valorisation. The Ardèche département has acquired the La Boissine domain including the Lagerstätte in 2005 as part of its policy of nature safeguarding, on both biodiversity and geodiversity aspects. The aims are (1) the protection of the fossiliferous site, (2) the improving of the scientific knowledge and (3) the opening to the public. In that view, the Ardèche département and the municipality of La Voulte-sur-Rhône are leading a scientific and tourist development program of the La Boissine domain.

A fence has been put up on the La Boissine domain to control the access to the Lagerstätte and to buildings intended to accommodate the public and the scientists. In a scientific view, the Ardèche département and the municipality of La Voulte-sur-Rhône plans to collaborate with research institutions for organizing palaeontological excavations from 2014 and to provide access to the fossil collections. Scientists, whether they come for making excavations or for visiting the collections, have at their disposal tools for the fossil cleaning, a scientific library and desks to work. From spring 2014, the public will discover in the La Boissine domain next to the Lagerstätte the new Museum of Palaeontology of La Voulte-sur-Rhône. The exhibition concerns the Konservat-Lagerstätten, as very scarce and peculiar fossiliferous sites, and tackles the processes which have led to the exceptional preservation and the very detailed information they provide for the accurate reconstruction of paleoenvironments and for the understanding of the evolution of life on Earth. A large part is devoted to the La Boissine domain (geology, history of iron ore mining) and to the La Voulte Lagerstätte soft-bodied fossils. Particular attention is given to the accessibility for all publics, profane as warned (workshops for children, tours), in order to raise public awareness of the importance of preserving geodiversity.

7. Conclusion

In conclusion, the La Voulte Lagerstätte provides key-information on the palaeobiodiversity during Jurassic. If the interpretations recently proposed are correct, the La Voulte Lagerstätte may be considered as a very rare and precious witness of the bathyal Mesozoic communities. The future excavations (summer 2014) will probably bring new data and reinforce our knowledge of this unique Jurassic biota.

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